A NEW ENTOPROCT-LIKE ORGANISM FROM THE BURGESS SHALE OF BRITISH COLUMBIA

by s. conway morris

Abstract. *Dinomischus isolatus* gen. et sp. nov. is described from the Burgess Shale (Middle Cambrian). A calyx, supported by a long slender stem, bears distally a circlet of elongate bracts which may have been used in filter feeding. Within the calyx a recurved gut with enlarged stomach is supported in a spacious body cavity by suspensory fibres. A sessile mode of life comparable to that of the modern pennatulacean *Umbellula* (Cnidaria) is proposed. Certain similarities with other stalked animals, especially the Entoprocta, exist. The actual affinities of *D. isolatus* remain, however, uncertain.

A l t h o u g h some 90% of the Burgess Shale fauna has received at least a preliminary description a number of animals, usually represented by only a few specimens, have remained undescribed. The present paper delineates one such new genus and species. Three specimens, all lacking their counterparts, of this new creature are known. One specimen has been located in the National Museum of Natural History (formerly the United States National Museum, USNM), Washington, D.C., and another in the Royal Ontario Museum (ROM), Toronto during searches through the collections of Burgess Shale material in these institutions. Dr. D. E. G. Briggs kindly drew the attention of the author to a third specimen in the Museum of Comparative Zoology (MCZ), Harvard. The USNM specimen had evidently been noted by C. D. Walcott, who discovered the Burgess Shale and described much of its fauna and flora, because a retouched photograph was found beside the specimen. However, neither Walcott nor any other worker has published any information on this animal.

The history of excavation of the Burgess Shale and its stratigraphic setting were briefly reviewed by Conway Morris (1976*a*). The USNM specimen is labelled 35k, which is that institution's locality number for the Phyllopod bed exposed in the Burgess quarry (Walcott 1912). It was from this quarry that Walcott recovered, during several seasons (1910–1913, 1917) of collecting, the great majority of fossils with their soft parts preserved. No information on the stratigraphic position of this specimen within the 2·31 m (7 ft 7 in.) thick Phyllopod bed is available. Presumably the MCZ specimen was found by the Harvard team during their expedition to the Burgess Shale exposures in 1930 (Raymond 1935). Although fossil material was obtained from the Burgess quarry, they also collected a substantial number of specimens in a higher quarry (USNM locality 35k/10) which is situated some 19·8 m (65 ft) above the Burgess quarry. Walcott had recovered some fossils from this excavation which is generally known as Raymond's quarry. The matrix surrounding the MCZ specimen is lithologically similar to the rocks exposed in Raymond's quarry. The MCZ specimen may, therefore, have come from this higher horizon in the Burgess Shale. The ROM specimen was collected in 1975 from talus material which had been discarded from the two quarries by previous expeditions: more precise stratigraphic information is unavailable (D. Rudkin pers. comm.).

A note on the photography and interpretation of the specimens.

All three specimens have been photographed in ultra-violet light under a directional lamp using Panatomic-X film. Plate 112, figs. 1, 3, 5, 6 were photographed in high-angle light. The lamp was inclined to the horizontal specimen at about 60°. The specimen was then tilted through about 10° towards the lamp until maximum reflectivity, as observed down the focusing tube, was obtained. Plate 112, figs. 2, 4 were photographed in low-angle light. The inclination of the lamp was about 30° and the specimen was placed as horizontal as possible. Focusing was undertaken in ordinary light.

Camera-lucida drawings (text-fig. 2A, B) are placed opposite Plate 112 as a guide to the interpretation of figs. 1–5.

SYSTEMATIC PALAEONTOLOGY

Phylum UNCERTAIN
Family DINOMISCHIDAE fam. nov.

Diagnosis. Long slender stem supporting calyx with distal circlet of bracts which apparently encloses both openings of the recurved gut.

Genus DINOMISCHUS gen. nov.

Type and only known species. Dinomischus isolatus sp. nov.

Derivation of name. The generic name is derived from Dinos (Greek—goblet) and Mischos (Greek—stalk or stem) and refers to the similarity to a hock glass.

Diagnosis. Sessile non-colonial metazoan. Body consists of calyx supported by elongate stem. Calyx bears about twenty elongate bracts which project distally. Calyx otherwise smooth, without plates or spines. Gut recurved with prominent saccular stomach supported in body cavity by suspensory fibres. Stem enlarged immediately beneath calyx, otherwise straight and slender, terminating in slightly swollen holdfast.

Dinomischus isolatus sp. nov.

Plate 112; text-fig. 2A, B

Derivation of name. isolatus (NL) refers to the non-colonial nature of the animal.

Diagnosis. As for the genus.

Holotype. USNM 198735 from the Stephen Formation (Middle Cambrian), Burgess Shale member (*Pagetia bootes* faunule of the *Bathyuriscus-Elrathina* Zone: Fritz 1971), Field, southern British Columbia.

Paratypes. MCZ 1083, ROM 32573.

Preservation. The specimens are preserved as very thin films in the same manner as the majority of Burgess Shale species (Whittington 1971a, b, 1974, 1975a, b; Hughes 1975). The films, which have a siliceous composition (Conway Morris 1977), are in part darker than the surrounding rock matrix, but certain features such as the gut, suspensory fibres, and stem are preserved as reflective areas. The specimens are isolated on small slabs and none is associated with any other identifiable fossils.

The preservation of the USNM specimen is superior to the others and features of internal anatomy are comparatively clear. This variation in preservational quality may be largely ascribed to the amount of decay that occurred prior to fossilization.

Morphology. The probable appearance of the animal is shown in text-fig. 1, which is drawn in the style of a partial dissection. The body can be divided into a calyx and slender stem. Dimensions of the principal parts of the body are given in Table 1. In the ensuing discussion the stem is assumed to have supported the calyx above the sea-floor. Thus upper and distal, and lower and proximal are taken to be synonymous. The terms dorsal and ventral are not used because of the impossibility of determining which side was in fact directed towards the sea-floor. The entoprocts, for instance, are attached to the stalk on what is morphologically their dorsal side (Harmer 1886).

TABLE 1. Dimensions of various parts of the body of *Dinomischus isolatus* gen. et sp. nov. All readings in mm.

Feature	USNM 198735	MCZ 1083	ROM 32573
Length of calyx up to base of bracts	5·4	3·8	4·8
Length of bracts	4·5	2·7	4·2
Width of bracts	0·7	0·6	0·6
Length of upper stem	2·8	*c.* 1·4	*c.* 2
Length of lower stem	5·1+	12	16·5+
Width of lower stem	0·5	0·3	0·4
Length:width of lower stem	10·2+	40	41·2+
Length of basal holdfast	—	2	—
Width of basal holdfast	—	0·7	—

The over-all shape of the calyx was a rounded cone. It is assumed that the roof of the calyx was flat (text-fig. 1). Slight variations in calyx shape have, however, been noted. In the MCZ specimen the calyx increases in width noticeably towards the distal end (Pl. 112, figs. 3, 4; text-fig. 2B), whereas in the ROM specimen it is narrower and the sides diverge only slightly (Pl. 112, fig. 6). The calyx of the USNM specimen appears to represent an intermediate case (Pl. 112, figs. 1, 2; text-fig. 2A). This variation may be a reflection of the calyx being originally laterally compressed so that its cross-section was elliptical. Alternatively, the walls of the calyx may have been sufficiently pliable to allow the calyx shape to be controlled by muscular contraction. With this latter alternative in mind it may not be coincidental that in the narrow ROM specimen the calyx bracts (see below) are clustered together (Pl. 112, fig. 6), while in the broad MCZ specimen the bracts diverge from one another (Pl. 112, figs. 3, 4; text-fig. 2B).

The calyx bore prominent plate-like structures, termed here the calyx bracts, which arose from about two-thirds above its base. They appear to have been rather rigid and were probably thin and plate-like. They are not, therefore, considered to have been true flexible tentacles. The bracts were elongate, with smooth edges and pointed distal terminations (Pl. 112, figs. 1–4, 6; text-fig. 2A, B). In the USNM specimen the distal left-hand edge of some of the bracts is deflected inwards so giving them an asymmetrical appearance (Pl. 112, figs. 1, 2; text-fig. 2A). This feature may be due to partial decay and is not regarded as original. The distal extension of the gut past the insertion points of the bracts (Pl. 112, fig. 1; text-fig. 2A) indicates that they probably mantled the upper part of the calyx, although it is impossible to determine whether the inner surfaces of the bracts were firmly attached to the outer wall of the calyx. Distally the bracts projected beyond the calyx (text-fig. 1). Nine bracts have been noted in the USNM specimen. It is believed that they represent the complement
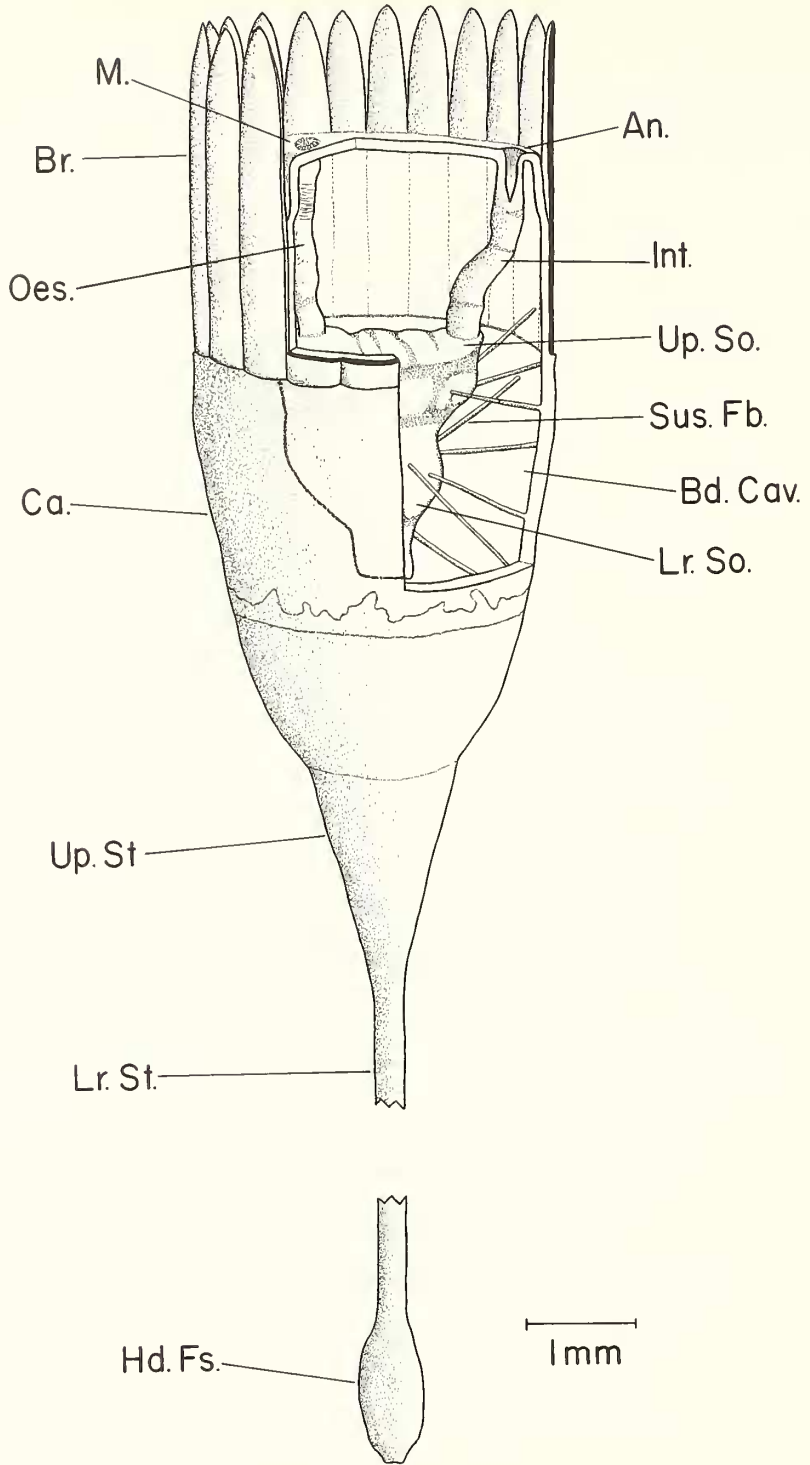
of one side of the animal so that the total was about twenty. The bracts apparently encircled the calyx and there is no evidence of any interruption or gap. The overlap (Pl. 112, figs. 1, 2; text-fig. 2A) and separation (Pl. 112, figs. 3, 4; text-fig. 2B) of adjacent bracts demonstrates that they were not fused into a single collar-like structure. There is no clear evidence that the bracts were connected by a membranous structure and it is probable that each bract was separately inserted on to the calyx wall. Below the insertion line of the bracts the calyx was smooth and lacked spines, plates, or other ornamentation.

Features of the internal anatomy of the calyx are comparatively well preserved in the USNM specimen. The upper calyx is occupied by a reflective mass whose shape can be resolved into a U with a greatly thickened base (Pl. 112, fig. 1; text-fig. 2A). This feature is interpreted as a recurved gut. The two vertical limbs of the U, taken to be extensions of the gut, appear to have been simple tubes. They are regarded here as the oesophagus and intestine which opened on the roof of the calyx at the mouth and anus respectively (text-fig. 1). The more median branch of the gut is taken to be the oesophagus (Pl. 112, fig. 1; text-fig. 2A), because it is reasonable to imagine the mouth in a more central position so as to accept food from all sides. The eccentric branch that ran close to the edge of the calyx is taken to be the intestine (Pl. 112, fig. 1; text-fig. 2A). The anus would thus have been situated near the margin of the animal to avoid fouling (text-fig. 1). Adjacent to the anus the bracts may have been absent, reduced, or more widely spaced to facilitate dispersal of waste matter. No direct evidence is, however, available.

The centrally positioned mass (i.e. the thickened closure of the U: Pl. 112, fig. 1; text-fig. 2A) is interpreted as the stomach (text-fig. 1). On the basis of slight variation in the reflectivity of the fossil film the stomach may be divided into a narrow upper region and a larger lower unit which narrowed proximally to a square-shaped termination. This lower region is regarded as a sac-like extension of the stomach.

The more diffuse reflective areas in the upper calyx of the other specimens are also interpreted as poorly preserved remnants of the gut (Pl. 112, figs. 3, 6; text-fig. 2B).

The space between the gut and the edges of the calyx is traversed by about fifteen reflective strands that radiate from the lower stomach (Pl. 112, fig. 1; text-fig. 2A). The arrangement of these strands suggests that they were suspensory fibres or muscles which helped to support the stomach (text-fig. 1). Their distribution does not uphold the idea that they were either body-wall or retractor muscles. Their presence strongly suggests that the gut was suspended in a fluid-filled body cavity.

Immediately beneath the proximal extension of the stomach the lower calyx is preserved as a reflective film. The upper margin of this film is highly irregular and is distinctly more reflective than the remainder of the lower calyx (Pl. 112, fig. 1; text-fig. 2A). The significance of the reflective preservation within the lower calyx is


TEXT-FIG. 1. Reconstruction of appearance of *Dinomischus isolatus* gen. et sp. nov. A portion of the upper calyx and bracts has been cut away to reveal internal details. The groove separating the upper calyx wall from the bracts is hypothetical. Most of the lower stem has been omitted. The holdfast is inflated to its maximum size. An., anus; Bd. Cav., body cavity; Br., bract; Ca., calyx; Hd. Fs., holdfast; Int., intestine; Lr. So., lower stomach; Lr. St., lower stem; M., mouth; Oes., oesophagus; Sus. Fb., suspensory fibres; Up. So., upper stomach; Up. St., upper stem.
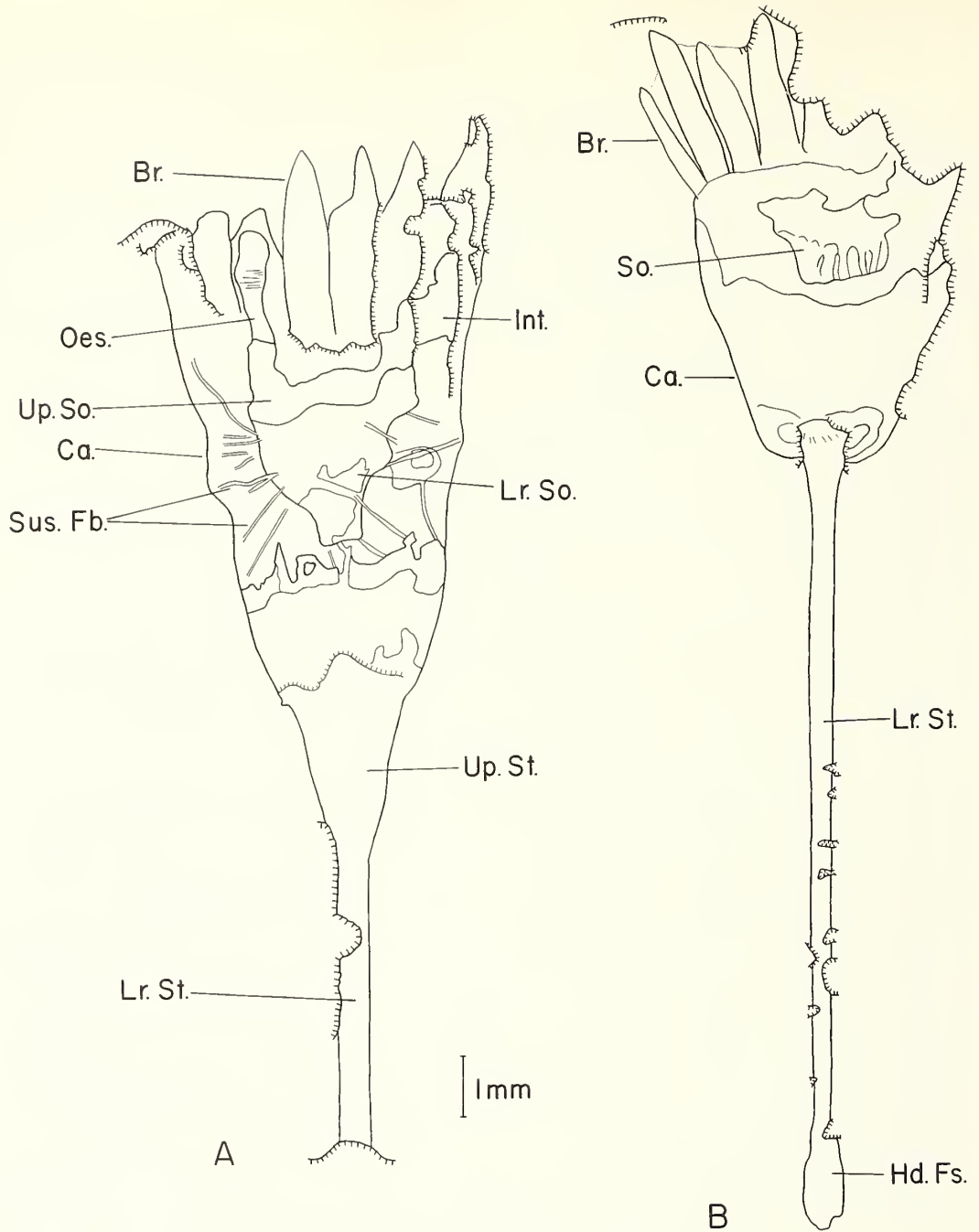
TEXT-FIG. 2. Camera-lucida drawings. Lines with hachures indicate definite breaks in slope, the hachures being directed downslope. A, USNM 198735. B, MCZ 1083. So., stomach. See text-fig. 1 for other abbreviations.

EXPLANATION OF PLATE 112

Figs. 1-6. *Dinomischus isolatus* gen. et sp. nov. USNM 198735 (holotype), figs. 1–2; MCZ 1083 (paratype), figs. 3–5; ROM 32573 (paratype), fig. 6. All photographs taken under ultra-violet light. 1, high-angle light from east, ×4. 2, low-angle light from east, ×4. 3, high-angle light from south-west, ×6. 4, low-angle light from south-east, ×6. 5, enlargement of proximal holdfast, high-angle light from north-east, ×16. 6, high-angle light from north-west, ×6.

PLATE 112
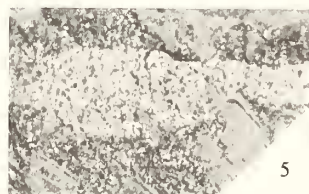
CONWAY MORRIS, *Dinomischus*

uncertain. It could, for example, represent body-wall muscles or even reproductive organs. It is not known whether the body cavity extended into this part of the calyx.

The stem was attached to the undersurface of the calyx (Pl. 112, figs. 3, 4; text-fig. 2B), presumably in its centre. It can be divided into three sections: a short upper section, a lower slender section, and a proximal holdfast. The width of the upper stem increased distally, but it was demarcated from the calyx by a distinct change in width (Pl. 112, figs. 1, 2, 6; text-figs. 1, 2A). Its union with the rest of the stem was, however, less abrupt (Pl. 112, figs. 1, 2, 6; text-figs. 1, 2A). The upper and lower stem are preserved as a uniform reflective film. This similarity in preservation indicates that it would be incorrect to take the upper stem as a proximal extension of the calyx. The lower stem is remarkable for its length, straightness, and slender proportions as compared with the size of the calyx it supported (Pl. 112, figs. 3, 4, 6; text-fig. 2B). It was of more or less constant width and probably had a circular cross-section. The surface of the lower stem appears to have been smooth. No internal structures such as supporting skeletal tissue or canals are preserved. The basal stem consisted of a slightly swollen holdfast which lacked rhizoids or additional attachment devices (Pl. 112, fig. 5; text-fig. 2B).

DISCUSSION

Mode of life. Recent work (Whittington 1971a, b, 1974, 1975a, b; Hughes 1975; Conway Morris 1976b) on other members of the Burgess Shale fauna has shown that features such as the variable orientation of specimens with respect to the bedding plane and the separation of appendages by sediment are best explained by transport and burial in mudflows which probably did not extend very far above the sea-bed. It has become clear that the majority of Burgess Shale species suffered this burial history and must, therefore, have been benthonic. The specimens of *D. isolatus* are preserved parallel to the bedding plane and do not show any evidence as to their taphonomy, unless the imbrication of the bracts of the USNM specimen (Pl. 112, figs. 1, 2; text-fig. 2A) is ascribed to the effects of transport in a mudflow. However, the elongate stem with holdfast was presumably used to support the calyx and this strongly suggests that *D. isolatus* was a member of the sessile benthos.

It is most probable that *D. isolatus* either lived on the muds that slumped into the area where the Phyllopod bed was being deposited or was overwhelmed by mudflows descending from further upslope. The scarcity of this creature and its apparently isolated occurrence might suggest that it was not gregarious and its original distribution over the sea-floor was very sparse. Alternatively, the rarity of *D. isolatus* may be due to infrequent disturbance by the mudflows. The Phyllopod bed was deposited in deep water close to a prominent carbonate bank (Fritz 1971). *D. isolatus* might have lived on parts of the bank, such as a basal apron, which generally remained clear of basinal mudflows.

On first consideration the length to width ratio of the stem (Table 1) appears to be high in relation to the size of the calyx. It is possible that the stem was deeply embedded in the sediment. The functional advantage of a largely buried slender stem over a thicker and shorter stalk is, however, difficult to imagine. As is discussed below several phyla have representatives with attenuated attachment devices that serve to

keep the animal clear of the sea-floor. It is, therefore, suggested that most of the stem was free of the sediment. The exact depth of penetration might have depended to some extent on its rigidity, but it should be remembered that the sea-water would have counterbalanced most of the calyx weight. The straightness of the stem (Pl. 112, figs. 3, 4, 6; text-fig. 2B) indicates that it was rather inflexible, although this may be a post-mortem effect. Rigidity of the stem may have been produced by supporting tissue, such as a collagenous or chitinous endoskeleton, or turgor pressure derived from an internal canal. These two mechanisms need not have been mutually exclusive and may have complemented one another. As noted above there is, however, no direct evidence of any skeletal support. The action *D. isolatus* took to avoid being scoured out by strong currents or overwhelmed with sediment is conjectural. The holdfast, or even the stem, may have been sufficiently muscular to drag the animal upwards or downwards.

Although a number of animals support the body on a slender stalk of varying flexibility, the mode of attachment of *D. isolatus* would seem to have its closest analogue in the modern deep-sea *Umbellula* (Cnidaria: Pennatulacea) (Kölliker 1880; Hickson 1916; Broch 1958). In this sea-pen a rosette of large feeding polyps or auto-zooids is supported by a long slender stalk or peduncle which is embedded in soft sediments with the aid of a muscular bulb. As in *D. isolatus* the terminal bulb lacks additional attachment devices such as rhizoids. The peduncle can be up to 1 m long and is supported by water-filled gastrovascular canals and a skeletal axis, which in *Umbellula* is variably calcified (Broch 1958). Although the peduncle is flexible it can achieve sufficient rigidity to keep the autozooids well clear of the sediment (Jahn 1970, fig. 2; Menzies *et al.* 1973, figs. 5-25, 5-26b, 7-15c).

It is proposed that the calyx bracts were involved in feeding. As is stated below there is no evidence that the animal possesses a tentacular feeding device, and *D. isolatus* does not appear to have any other organ more suitable for collecting food. As is noted above the bracts are not considered to be genuine tentacles. The rigidity of the bracts indicates that they were unable to enfold or grasp prey, and it is more probable that they were ciliated so that food was swept, perhaps with the aid of mucous secretions, to the mouth. *D. isolatus* is, therefore, regarded as a microphagous suspension feeder. The feeding position may be represented when the bracts are spread outwards (Pl. 112, figs. 3, 4; text-fig. 2B). The observation that the bracts originate at points rather low on the sides of the calyx is difficult to explain if their proposed use as food collectors is correct. One possibility is that a deep, perhaps ciliated, gutter or groove separated the bracts from the calyx (text-fig. 1). Alternatively, only the distal part of the bracts may have been involved in feeding. Ciliary currents may have also dispersed faeces.

Zoological affinities. A number of phyla or groups within a phylum have adopted the groundplan of a body, generally cup-like, supported by an elongate stem. Examples may be found in the sponges, cnidaria, tunicates, echinoderms, and entoprocts. *D. isolatus* has at least superficial similarities to these groups as well as the ectoprocts, but important differences remain.

1. Stalked sponges such as *Hyalonema* (Laubenfels 1955) have a much simpler organization than *D. isolatus* and no realistic comparison is possible. The similarity

to stalked cnidarians such as the Hydroida, Stauromedusae, and Pennatulacea, e.g. *Umbellula* would also appear to be purely superficial. The presence of a recurved gut with separate mouth and anus is clearly more advanced than the body plan of the Cnidaria.

2. Similarly, no close resemblance can be demonstrated between *D. isolatus* and stalked tunicates such as *Boltenia* and *Culeolus* (Herdman 1882).

3. A number of Middle Cambrian echinoderms possess either variously developed aboral extensions of the calyx termed holdfasts or else true stems (Sprinkle 1973). They are represented by the eocrinoids, e.g. *Akadocrinus*, *Gogia*, and the earliest known crinozoan (?crinoid), *Echmatocrinus brachiatus*, which is also from the Burgess Shale (Sprinkle 1973). Comparisons show that no genuine affinity exists between these echinoderms and *D. isolatus*. A major difference is the absence of calcareous plates and ossicles in the calyx and stem.

4. A closer comparison is, however, possible with the Entoprocta and Ectoprocta (or Bryozoa). A number of workers believe that entoprocts and ectoprocts have developed different grades of organization from a common, but distant, proto-stomatous ancestor (Brien and Papyn 1954; Hyman 1959). Opinion differs, however, as to the exact degree of affinity between the two groups. Some authors have suggested that there are sufficient similarities to place the entoprocts in the Bryozoa (Marcus 1939; Nielsen 1971). The majority of workers are more impressed by the numerous differences between the entoprocts and ectoprocts (Atkins 1932; Hyman 1951; Brien 1960, 1970; Brien and Papyn 1954), and the former group is now usually placed in a phylum of its own.

The entoprocts are a minor marine and freshwater group of small (seldom above 5 mm long) animals. The solitary Loxosomatidae are regarded as the most primitive family (Hyman 1951; Brien 1960), whilst the Pedicellinidae and Urnatellidae are believed to represent successively more evolved families that became colonial. The more recently described Loxokalypodidae (Emschermann 1972) may represent a group intermediate between the Loxosomatidae and the latter two families. Helpful accounts of entoproct morphology are available in Hyman (1951) and Mariscal (1965). The bilaterally symmetrical body consists of a slightly laterally compressed calyx supported by a stalk. The calyx bears a circle of ciliated tentacles. In the solitary loxosomatids the stalk is attached to the substrate by an adhesive disc. The stalk of the colonial entoprocts, however, often has a swollen muscular attachment to the stolon. The gut is recurved with both the mouth and anus opening within the circle of tentacles. The body cavity, which extends into the tentacles, is a pseudocoel that is filled with a gelatinous substance containing mesenchyme cells.

D. isolatus has superficially, at least, a certain resemblance to an individual ento-proct: both groups being characterized by a calyx, stem, and recurved gut. Neverthe-less there are some differences. The individual entoproct is over five times smaller than *D. isolatus*. The calyx bracts do not appear to be true tentacles, although like those of an entoproct they apparently encircled both mouth and anus. The ancestral entoproct conceivably had a fluid-filled pseudocoel, but extensive development of mesenteries and suspensory fibres is not typical of other pseudocoelomate animals. In some entoprocts fibres run from the calyx wall to the mouth and oesophagus, but the rest of the gut receives no such attachment. It is concluded that the similarities

may indicate that some degree of affinity, albeit distant, exists between *D. isolatus* and the entoprocts. One possibility is that present-day entoprocts are miniaturized descendants of a dinomischid-like creature.

5. The ectoprocts are always colonial and the individual animals (zooids) are usually encased in a tough exoskeleton. Useful summaries of this group are given by Hyman (1959) and Ryland (1970). A typical unmodified autozooid of the colony bears a horseshoe-shaped or circular ring of tentacles, the lophophore, which embraces the mouth. As the gut is strongly recurved the anus opens close to the lophophore. The lophophoral tentacles arise from an introvert-like structure which when withdrawn by the retractor muscles forms the tentacle sheath. The body cavity is regarded as a true coelom.

D. isolatus has certain similarities to an individual autozooid. The saccate nature of the stomach has a parallel in the ectoproct caecum which forms a prominent extension of the stomach. The caecum is attached to the zooid base by a strand of tissue—the funiculus. The trunk coelom is sometimes traversed by peritoneal strands and muscle fibres, but an exact parallel to the suspensory fibres of *D. isolatus* does not appear to exist. The calyx bracts cannot be directly compared with the lophophore. The anus of *D. isolatus* appears to have opened within the circle of bracts and it is very unlikely that they were deflected around the anus to give a horseshoe shape. In a few ectoprocts, e.g. *Bowerbankia* (Ctenostomata) the proximal tentacle sheath is surrounded by a collar which pleats upon retraction of the tentacles and might then superficially resemble the circlet of calyx bracts. Even were it assumed that the bracts are equivalent to the collar, there is no evidence for a tentacular organ in *D. isolatus* that might be compared with the lophophore.

In over-all appearance the autozooids show a less striking resemblance to *D. isolatus* than do the entoprocts. In particular the autozooids always lack a stem, even when they have separate insertions on the stolon. The autozooids are, moreover, about ten times smaller than the individuals of *D. isolatus*. It may, therefore, be concluded that no actual affinity exists between *D. isolatus* and the ectoprocts.

Farmer *et al.* (1973) suggested that the ancestral ectoproct was a solitary phoronid-like creature which underwent simplification and a marked reduction in size when it adopted a colonial way of life. *D. isolatus* evidently differs in too many features to be even considered as an ancestral ectoproct.

6. A comparable example deserving examination is *Escumasia roryi* Nitecki and Solem, 1973. This curious animal is characterized by a flattened sac-like body with two distal tentacles situated either side of the mouth. The body was supported by a slender stem that had a proximal attachment disc. The gut was apparently large and the anus was situated on the side of the body. Nitecki and Solem (1973) were unable to assign this animal to any known phylum, although they made certain comparisons with the Cnidaria. No close affinity exists between this creature and *D. isolatus*.

Although the phyletic position of *D. isolatus* remains unresolved, the author believes that the closest affinities of this creature may possibly lie with the entoprocts. However, descriptions of other animals from the Burgess Shale (Whittington 1975*a*; Conway Morris 1976*a, b*, 1977) as well as from younger Palaeozoic rocks (Johnson and Richardson 1969; Davis and Semken 1975) are a useful reminder that not all fossils can be directly accommodated in extant phyla.

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S. CONWAY MORRIS

Department of Geology
Sedgwick Museum
University of Cambridge
CB2 3EQ